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Mesoscale subduction at the Almeria-Oran front. Part 2: biophysical interactions.

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Abstract

The Almeria-Oran front forms where surface waters of Atlantic and Mediterranean origin meet at the eastern end of the Alboran Sea. A multidisciplinary field experiment on RRS *Discovery* in December 1996, in the second observational phase of the EU funded OMEGA project, observed the biological impact of mesoscale frontal instability of the Almeria-Oran frontal jet. It is concluded that periodic vertical velocities of ~ 20 m/day, associated with the propagation of wave-like meanders along the front, have a significant effect on the vertical distribution of zooplankton across the front despite their ability to migrate at greater speeds. Observations of a layer of fluorescence coincident with subducted surface waters indicated that phytoplankton were drawn down and along isopycnals, by cross front ageostrophic motion, to depths of 200 m. From the study of sound scattering layers identified in acoustic backscatter data a layer of zooplankton was found coincident with the drawn down phytoplankton. This layer persisted during and despite diel vertical migration. High resolution optical plankton counter data showed smaller zooplankton, that did not undertake diel vertical migration, remained concentrated near the surface in the fast flowing frontal jet.

Keywords: OCEANIC FRONTS, BIOACOUSTICS, MESOSCALE FEATURES, VERTICAL MOTION, BIOPHYSICAL INTERACTIONS, PLANKTON

DISTRIBUTIONS, MEDITERRANEAN SEA, WESTERN MEDITERRANEAN, ALBORAN SEA, ALMERIA-ORAN FRONT, 2.5° W - 0.5° E, 35.0° N - 37.5° N.

1. Introduction

Fronts form at interfaces between different water masses of different hydrographic/dynamic properties (Sournia, 1994) and can often be characterised by a rapid change in the horizontal density gradient. Frontal zones harbour ecosystems where the patchiness of marine populations can be affected by the complex physical environment (Owen 1981; Haury, 1982).

Enhancement of primary producers in the proximity of fronts has been reported by numerous authors (Bainbridge, 1957; Olson, 1986; Strass, 1992 and others). This increase in biomass is thought to result from various mechanisms including: vertical motion affecting the light field encountered by phytoplankton (Lillibridge, 1990); mixing of phytoplankton and nutrients along the frontal interface (Yoder *et al.*, 1983; McClain *et al.*, 1990; L'Heguen *et al.*, 1993); death and subsequent remineralisation of foreign populations supporting higher endemic species growth, and along front advection of populations in the presence of an along front gradient in other environmental parameters (Olsen *et al.*, 1994). In ageostrophic fronts, where cross-frontal secondary circulation exists, this production can be exported downwards along sloping isopycnals (Dewey *et al.*, 1991; Gorsky *et al.*, 1991; Videau *et al.*, 1994).

This enhanced phytoplankton standing stock may be passed to higher trophic levels (Le Fevre, 1986). Zooplankton populations have been shown to be influenced by fronts in passive response to physical factors, or through behavioural changes (e.g. Boucher, 1984; Govini and Grimes, 1992; Ashjian, 1994; Thibault *et al.*, 1994). Enhancement of zooplankton abundance at frontal boundaries has been attributed to: behaviourally mediated concentration in the presence of convergence zones (Okubo, 1978; Olson and Backus, 1985; Franks 1992; 1997; Govoni and Grimes, 1992); close association with thermal gradients (Ortner *et al.*, 1980; 1981; Magnuson *et al.*, 1981); orientation to density discontinuities (Murav'yev and Shirshov, 1984) or abundance of food (Bowman and Esaias, 1978; Crowder and Magnuson, 1983). Interpreting

zooplankton distributions can be further complicated by zooplankton behaviour such as diel migration (e.g. Owen, 1981; Wishner and Allison, 1986). This paper describes phytoplankton and zooplankton distributions with respect to the hydrographic environment at the Almeria-Oran front in the Alboran Sea during December 1996.

The upper ocean circulation of the Alboran Sea is generally well known (Gascard and Richez, 1985; Perkins *et al.*, 1990; Sournia 1993; Prieur and Sournia, 1994; Folkard *et al.*, 1994). The Atlantic inflow enters the Western Mediterranean through the Strait of Gibraltar. Two anticyclonic gyres form in the Alboran basin, fed by this Atlantic inflow (**Figure 1**) (Tintore *et al.*, 1988; Allen *et al.*, 2001-this issue). The eastern Alboran gyre has been known to break down on occasions (Cheney and Doblal, 1982; Perkins *et al.*, 1987; Heburn and La Violette, 1990) and, as many as three gyres have been observed through satellite imagery (Viudez *et al.*, 1998). During its eastward migration, inflowing Atlantic Water (AW) is modified by upwelled Levantine Intermediate Water (LIW) and a Temperature Minimum Layer (TML) forming Modified AW (MAW). Satellite imagery indicates that MAW follows a number of paths around the Alboran Sea until reaching Cape Gata, where it meets Mediterranean Surface Waters (MSW) flowing slowly west (Figure 1 in Allen *et al.*, 2001-this issue). The convergence of these two water masses causes the MAW to be deflected southward towards Oran (Algeria) along the eastern edge of the Eastern Alboran Gyre, forming a well defined frontal zone (Tintore *et al.*, 1988). Physical and biochemical data indicate that the front is limited to the upper 200 m, with a strong southeastward geostrophic baroclinic jet (Folkard *et al.*, 1994). The secondary ageostrophic circulation associated with instability of the jet is characterised by surface convergence and periodic isopycnal sinking and upwelling (Tintore *et al.*, 1988; Allen *et al.*, 2001-this issue).

Frontal enhancement of phytoplankton populations has been observed at the Almeria-Oran front (Lohrenz *et al.*, 1988; Prieur and Sournia, 1994; Videau *et al.*, 1994; Fiala *et al.*, 1994). Diatom and nanoplankton abundance, chlorophyll content and primary production have been observed to be higher in the jet, either from satellite data (Arnone and La Violette, 1986; Lohrenz *et al.*, 1988; Arnone *et al.*, 1990) or in-situ shipboard data (Prieur *et al.*, 1993; Videau *et al.*, 1994; Fiala *et al.*, 1994). This

suggests that the frontal-jet system exhibits a fertilising effect on the otherwise oligotrophic waters of the Alboran Sea. Such a frontal enhancement is thought to result from the vertical input of nutrients caused by upwelling (Videau *et al.*, 1994; Fiala *et al.*, 1994; Claustre *et al.*, 1994) and this idea is supported by L'Helguen *et al.* (1992) and Videau *et al.* (1994) who observed a shallower nitracline in frontal waters than in Mediterranean waters (18-30 m and 30-60 m respectively). Numerical simulations undertaken by Zakardjian and Prieur (1994) support this hypothesis of production enhancement through vertical advection of nutrients. Videau *et al.* (1994) observed some of this enhanced production exported down below the thermocline to depths of 110 m, along the 28.0 σ_0 isopycnal.

Fewer studies have been made of the distribution of zooplankton at the Almeria-Oran front. Coincident with the observations of high phytoplankton biomass at the front during the project ALMOFRONT, Thibault *et al.* (1994) and Seguin *et al.* (1994) observed higher total standing stocks of zooplankton, including higher copepod abundances, in the frontal jet compared with surrounding waters. Baussant *et al.* (1993) investigated the distribution of micronekton and macrozooplankton using a 38 kHz echosounder, multi-net sampling and video profiling across the Almeria-Oran front. And showed that the region was dominated by several deep scattering layers, which could be attributed to *Cyclothone* fish or euphausiids.

As part of the EU MAST III funded project OMEGA (Observations and Modelling of Eddy scale Geostrophic and Ageostrophic motions), a multidisciplinary study was made of the Almeria-Oran front in December 1996 and January 1997. Concurrent physical, chemical and biological data were obtained on the same time and space scales. By using high-resolution modern biological sampling techniques with instruments such as a multifrequency echosounder, a Vessel-Mounted Acoustic Doppler Current Profiler (VM-ADCP) and an Optical Plankton Counter (OPC), detailed maps of the distribution of zooplankton were obtained. This paper compares the biological distributions (principally fluorescence, acoustic backscatter and OPC measured abundance and biovolume) with a knowledge of the physical environment (Allen *et al.*, 2001-this issue) and thus examines some of the biophysical interactions which occur at the Almeria-Oran front. In the next section we discuss the methods we

have used to collect biological information. In section 3 we present the results; in section 4, we present a discussion of our findings and make comparisons with previous work and, in section 5, draw our conclusions.

2. Materials and Methods

Hydrographic, bioacoustic and biological data were collected aboard RRS *Discovery* Cruise 224, the first part of which comprised the second field experiment of OMEGA between 22 November and 29 December 1996 (Allen *et al.*, 1997a). During the second half of RRS *Discovery* Cruise 224, 31 December 1996 to 17 January 1997, traditional deep nets were deployed in the region of the Almeria-Oran front (Pugh *et al.*, 1997).

Using the towed undulating vehicle SeaSoar (Pollard, 1986), two large scale and five repeat fine scale surveys were made of the Almeria-Oran front region in the western Mediterranean. In this paper we will concentrate on the data obtained during the three rapidly repeated fine scale surveys 1-3 (FSS1-3) (**Figure 2**). In addition to the usual CTD, used to determine hydrographic parameters, a fluorimeter, an irradiance (PAR) sensor and an Optical Plankton Counter (OPC) were used to determine fluorescence yield, light (Allen *et al.*, 1997b) and particle abundance in the size range 0.3 mm – 5.5 mm (Rabe *et al.*, 1998). Bioacoustic measurements were obtained using a hull mounted RDI 150 kHz VM-ADCP and a SIMRAD EK500 multifrequency echosounder (Crisp *et al.*, 1998; Crisp, 1999).

The repeated fine scale surveys had 10-11 parallel tracks, ~10 km apart, targeted at the Almeria-Oran front by near real-time analysis of underway thermosalinograph (TSG) data and AVHRR SST satellite imagery (Allen *et al.*, 1997a). Between surveys, CTD stations and biological sampling with targeted Longhurst Hardy Plankton Recorder (LHPR) tows were carried out to determine nutrient profiles and verify biological distributions indicated by the OPC and acoustic data. The timetable and duration of FSS 1-3, and five CTD stations that we refer to later, were as follows:

18:30 GMT 11/12/96 – 10:00 GMT 15/12/96 Fine Scale Survey 1 (FSS1)

18:40 GMT 15/12/96 – 04:05 GMT 16/12/96 CTD stations 37-41

21:10 GMT 16/12/96 – 17:30 GMT 20/12/96 Fine Scale Survey 2 (FSS2)

19:50 GMT 21/12/96 – 22:15 GMT 24/12/96 Fine Scale Survey 3 (FSS3)

CTD stations 37-41 (RRS *Discovery* station numbers 13037-13041), were carried out in a line across the centre of the Almeria-Oran front at the following positions:

station 37	36° 10.1' N, 01° 51.4' W
station 38	36° 14.0' N, 01° 45.7' W
station 39	36° 17.5' N, 01° 40.1' W
station 40	36° 21.7' N, 01° 34.5' W
station 41	36° 25.4' N, 01° 28.8' W.

2.1. Hydrographic measurements.

Configured as described above, SeaSoar had a typical depth range of 0 - 370 m at a towing speed of 8 knots (4 m/s), using a fully faired conducting cable. A full description of the hydrographic data is given in Allen *et al.* (2001-this issue): we shall draw on conclusions from this accompanying paper later in the discussion (section 4). The fluorimeter (Chelsea Instruments SubAquatracker) provided an indicator of phytoplankton biomass, and the data are presented in this paper in instrument volts.

2.2 OPC measurements.

A Focal Technologies Optical Plankton Counter (OPC) was mounted on a frame under the SeaSoar vehicle body. It was fitted with an acrylic insert to reduce the tunnel cross section to 0.001 m² for towed use (Pollard *et al.*, 2000). The OPC estimates the Equivalent Spherical Diameter (ESD) of particles which break a 640 nm wavelength LED light beam. The instrument is designed to resolve ESD's between 250 µm and 3 mm (Herman, 1992), which represent approximate lengths of 500 µm to 30 mm (Huntley *et al.*, 1995). Processing of the OPC data files followed the route developed by Pollard *et al.* (1996). Abundance and volume data were unrealistically low below 0.3 mm ESD and animals above 5.55 mm were too sparsely distributed to

be sampled effectively in the volume filtered. Thus measurements were separated into four size classes, 0.3 - 0.65 mm, 0.65 - 1.35 mm, 1.35 - 2.75 mm and 2.75 - 5.55 mm (ESD). Abundances and volumes for the first three size classes were averaged into 4 km along track by 8 m depth bins, consistent with the SeaSoar CTD data processing. Data for the largest size class were averaged into 12 km along track by 32 m bin depths to allow for the lower population density observed for larger zooplankton (Rabe *et al.*, 1998).

2.3 Acoustic measurements.

Acoustic backscatter data were recorded from a Vessel Mounted RD Instruments 150 kHz Acoustic Doppler Current Profiler (VM-ADCP) and a SIMRAD EK500 multifrequency (38, 120 and 200 kHz) echosounder.

2.3.1 VM-ADCP.

A number of authors have shown that acoustic backscatter data from a VM-ADCP may provide both quantitative and qualitative information about zooplankton distributions (Flagg and Smith, 1989; Plueddemann and Pinkel, 1989; Roe *et al.*, 1996; Griffiths and Diaz, 1996). For the duration of the SeaSoar surveys, we have calibrated acoustic backscatter strength as Mean Volume BackScatter (MVBS), corrected for the variation of the sound absorption coefficient with changing salinity and temperature (from *in situ* SeaSoar CTD data) following the method used by Roe *et al.* (1996). It was not possible to tow the LHPR at the same time as SeaSoar, therefore in-situ salinity and temperature from the environmental sensors on the LHPR were used to calibrate concurrent VM-ADCP MVBS data.

2.3.2 SIMRAD EK500.

The SIMRAD EK500 is a scientific multifrequency echosounder, operating at three frequencies, 38, 120 and 200 kHz. It has an extremely wide (150 dB) dynamic range which enables it to measure target strength reliably down to -120 dB and thus, as well as measuring individual targets, it is ideal for measuring Mean Volume BackScatter

(MVBS). The EK500 was housed in a towed fish deployed from its own portable winch over the port side of the after deck of RRS *Discovery*. MVBS data are presented here following the manufacturer's calibrations (Crisp *et al.* 1998).

2.4 LHPR measurements.

Between SeaSoar surveys the LHPR (Longhurst *et al.*, 1966; Williams *et al.*, 1983) was towed in a V-shaped profile across the Almeria-Oran front, typically through the upper 400 m of the water column. The samples were preserved onboard with 4% formaldehyde for the subsequent identification and counting of organisms on return to the Southampton Oceanography Centre (SOC).

3. Results

3.1 Physics

The Almeria-Oran front forms at the eastern boundary of the eastern of two Alboran Sea gyres (**Figure 1**). On the western side of the front, a high temperature, low salinity signature of Modified Atlantic Waters (MAW), present in the Eastern Alboran Gyre, was observed down to depths of ~200 m (**Figure 3**). The mixed layer depth decreases from west to east across the front. The frontal jet carries both MAW and higher salinity, but lower temperature (< 15.5 °C and 36.7-37.5 psu), Atlantic-Mediterranean Interface Waters (A-MIW, Gascard and Richez, 1985) eastwards into the W. Mediterranean forming the head of the Algerian current. Below the surface waters, a Temperature Minimum Layer (TML), of water with salinity of ~ 38.2 psu and temperature below 13.5 °C, was present to depths of 250-300 m. At maximum SeaSoar depths of ~370 m a signature of Levantine Intermediate Water (LIW) was observed. The water masses are discussed in detail in Allen *et al.* (2001-this issue), who follow Gascard and Richez (1985).

During RRS *Discovery* cruise 224, Mediterranean Surface Waters (MSW), characterised by high temperature and high salinity (> 37.5 psu), were observed to flow westwards along the south-east coast of Spain towards the Almeria-Oran front

region (Figure 8, Allen *et al.*, 2001-this issue). Between FSS2 and FSS3 a detailed analysis of the hydrography revealed the subduction and cross front transport of MSW on the $27.9 \sigma_0$ density surface, following the entrainment and advection of MSW into the frontal jet. Using MSW as a tracer, the observations suggested a vertical velocity component to the frontal flow of ~ 25 m/day. Detailed analysis (Allen *et al.*, 2001-this issue) further indicated that this vertical motion resulted from baroclinic instability of the Almeria-Oran front and the periodic propagation of regions of upward and downward motion along the front.

3.2. *Phytoplankton and nutrients.*

Fluorescence data indicated that phytoplankton were present throughout the mixed layer, with no distinct sub-surface maximum (**Figure 4**). It is interesting to note that the euphotic zone, as defined by the 1 W/m^2 isolume, only extends to ~ 50 m and therefore phytoplankton populations on the Alboran Gyre side of the front, where the mixed layer depth significantly exceeds the euphotic depth, may spend a significant time at low light levels. Vertical profiles of fluorescence yield from 5 CTD stations, carried out across the front between FSS1 and FSS2 (section 2), showed that phytoplankton were typically uniformly distributed above the nitracline, which was at a similar depth to the thermocline (**Figure 5**). The nitracline shelved from 70-100 m on the Alboran Gyre side of the front to 30-50 m on the Mediterranean side, following the change in mixed layer depth. Surface values of nitrate were typically $\sim 1 \mu\text{mol/l}$: below the nitracline, at 300 m depth, the nitrate concentration increased to $\sim 8 \mu\text{mol/l}$ (**Figure 5**).

The pattern of phytoplankton distribution following the mixed layer, and thus shoaling from west to east across the front, was consistent throughout the three fine scale surveys. During FSS3, however, distinct tongues of fluorescence were observed lying between the 27.4 and $28.4 \sigma_0$ isopycnals at the bottom of the thermocline, under the surface waters of the Alboran gyre and extending to depths of ~ 200 m (**Figure 4**).

3.3. *Zooplankton*

MVBS was obtained from acoustic backscatter data to describe the distribution of zooplankton, larger than a few millimetres in length, in the Almeria-Oran frontal region. We have identified three Sound Scattering Layers (SSL1, SSL2 and SSL3) in both ADCP and EK500 echosounder MVBS data.

SSL1 was a permanent feature occurring in 38 kHz EK500 data throughout the survey area between ~250 and >600 m. The maximum intensity of this layer typically occurred between 300 and 500 m and varied between -60 to >-56 dB, compared with background values of ~-95 dB (**Figure 6**). This layer was also present in data from the ADCP, near the limit of the instrument's depth range (**Figure 6**). There were no obvious variations in the depth of SSL1 either side of the front, although its intensity decreased at night.

SSL2 was present in both ADCP and EK500 data, at all frequencies. It does not refer specifically to a discrete layer but is used here to describe a diurnal signal. High backscatter was present at depth (typically >300 m) during the day, moving to the surface at night (**Figure 6**). At all frequencies night-time data were distinguished by the presence of high backscatter in surface waters, typically 20 – 30 dB higher than day-time values. The night-time patterns in EK500 MVBS data at 120 and 200 kHz were characterised by high backscatter throughout the surface with no discrete layering. However, ADCP and 38 kHz EK500 MVBS data were more structured, with a discrete layer of high MVBS occurring between the 27.4 and 28.4 σ_t isopycnal, referred to here as SSL3.

SSL3, was a recurring feature in both day and night MVBS data, but found only during FSS3. It was detected principally in ADCP and 38 kHz EK500 data sets because its depth was often below the acoustic penetration depth of the EK500 at the 120 and 200 kHz frequencies. SSL3 was concurrent with the tongue of high fluorescence (**Figure 4**) with a MVBS typically 9 dB greater than surrounding water, indicating an 8-fold increase in acoustic backscatter (a change of 3 dB is equal to a doubling of signal). This layer was present day and night and persisted despite and during the periods of diel migration (**Figure 6**).

Zooplankton biovolume, determined from LHPR samples, increased at the depth of SSL3 (**Figure 7**). Identification of zooplankton groups indicated an increase in the abundance of euphausiids and chaetognaths at the same depth as SSL3. Below 300 m, and coincident with SSL1 (**Figure 7**), fish dominated the biovolume in the net samples.

In addition to the identified sound scattering layers there was a patch of high MVBS which occurred consistently at the surface, in MAW, within the frontal jet. This patch of high backscatter was visible in both 120 and 200 kHz EK500 data (**Figure 8**) with a MVBS 12 dB greater than the surrounding waters. Coincident with the high MVBS within the frontal jet a high abundance of generally smaller particles was also observed in OPC data. A high particle volume ($\sim 4000 \text{ mm}^3/\text{m}^3$) compared with surrounding waters ($\sim 125 \text{ mm}^3/\text{m}^3$), within the total size range measured by the OPC (0.3 – 5.55 mm ESD), was concentrated above 50 m depth on the edge of the Alboran gyre. This increase in particle volume was most noticeable in the size range 0.65 – 1.35 mm and 1.35 – 2.75 mm ESD (**Figure 8**). This was the only distinct recurring pattern found in the OPC data; which did not contain a clear diel migratory signal or a noticeable increase in particle volume between the 27.4 and 28.4 σ_t isopycnal surfaces during FSS3.

4. Discussion.

The Almeria-Oran front forms where waters of Atlantic origin meet Mediterranean surface waters in the Alboran Sea, and its shape and position are variable on a time scale of days. In this study the front was found in its usual position as the eastern boundary of the eastern of two Alboran gyres (Tintore *et al.*, 1988; Folkard *et al.*, 1994; Prieur and Sournia, 1994; Allen *et al.*, 2001-this issue). The analysis of temperature and salinity on density surfaces showed Mediterranean Surface Water (MSW) advecting westward along the Spanish Coast until it reached the Almeria-Oran front. At this point, MSW became entrained into the frontal jet and advected with Modified Atlantic Waters (MAW) along the front. The surveys showed that instability of the front caused subduction of water down and across the front at an

observed subduction rate of ~ 25 m/day (Allen *et al.*, 2001-this issue). This subduction influenced the distribution of both phytoplankton and zooplankton at the front.

Fluorescence signals indicate that phytoplankton were present throughout the mixed layer in the survey area with no distinct subsurface chlorophyll maximum. This contrasts with previous work including the ALMOFRONT study where a distinct chlorophyll maximum was identified at the depth of the nitracline (DePalma *et al.*, 1987; Videau *et al.*, 1994). In the present study the nitracline coincided with the thermocline at the bottom of the mixed layer, but the surface layer values of $\sim 1 \mu\text{m}$ do not indicate severe nitrogen depletion. The nitrate concentrations reported in this study agreed with previously reported values (Bianchi *et al.*, 1994). In both the OMEGA and ALMOFRONT studies the nitracline shelved across the Almeria-Oran front from Atlantic waters to Mediterranean waters, although its depth was shallower during the ALMOFRONT study (18-30 m at the front, Videau *et al.*, 1994 compared with 30-50 m, this study). We believe that the deeper nitracline and more depth-independent fluorescence signal in the surface layers may be seasonally dependent due to entrainment of deeper waters through enhanced winter overturning.

In a significant number of the FSS3 legs, distinct signatures of phytoplankton subduction were seen in the contoured sections of fluorescence. High fluorescence was observed in layers coincident with the density surfaces $\sim 27.4 - 28.4$ extending to depths of up to 200 m, below the nitracline, euphotic zone and overlying Modified Atlantic Waters (MAW). This deep fluorescence maxima occurred coincidentally with the period of subduction of Mediterranean Surface Waters (MSW) discussed in Allen *et al.* (2001-this issue). The presence of phytoplankton at these depths occurring as a result of advection in between FSS2 and FSS3 is improbable, as ADCP showed no coherent residual signature of the strong along front flow below 150 m (Allen *et al.*, 2001-this issue). Phytoplankton are rapidly advected along the front by the frontal jet (speeds up to 1 m/s). Ageostrophic cross-front and vertical motion associated with periodic mesoscale instability of the front (Allen *et al.*, 2001-this issue) result in a downward and cross-front secondary transport of phytoplankton. Lohrenz *et al.*, (1988) previously observed chlorophyll maxima occurring along isopycnals on the Mediterranean side of the front, however this was attributed to the accumulation of

cells in a particular zone of density stratification (Hobson and Lorenzen, 1972). The present observations of layers of fluorescence coincident with the subducted MSW suggest that at least some phytoplankton were drawn down and along the isopycnals. Boucher *et al.* (1987), Dewey *et al.* (1991) and Hood *et al.* (1991) made similar observations of downward and oblique transport of phytoplankton along isopycnals. The subduction of phytoplankton at the Almeria-Oran front has been commented on previously, resulting in a virtual south-north transect of chlorophyll biomass (Figure 8 in Videau *et al.*, 1994) analogous to our in-situ fluorescence transects (**Figure 4**). Using estimates of vertical displacement rates Videau *et al.* (1994) calculated isopycnal descent rates to be 35 m/day, not dissimilar to the subduction rate of 25 m/day calculated and observed during this study (Allen *et al.*, 2001-this issue).

A permanent scattering layer below 300 m depth (SSL1) was observed in acoustic backscatter data from the ADCP and 38 kHz EK500 echosounder, within the TML and LIW. These observations were consistent with those of Baussant *et al.* (1993), who associated deep scattering layers at the Almeria-Oran front with non-migratory *Cyclothone* fish. Our LHPR net samples showed the presence of fish below 300 m and RMT catches, taken during leg 2 of RRS *Discovery* cruise 224 (Pugh *et al.*, 1997), contained numerous *Cyclothone* below 300 m (Howell, *pers comm.*). In this study the depth of SSL1 did not vary either side of the front, contrary to that reported by Baussant *et al.* (1993). This suggests that the non-migrating *Cyclothone* remained within the TML and LIW and that their distribution was not influenced by surface waters.

In addition to the permanent deep scattering layer (SSL1) a layer of high acoustic backscatter, shown in both ADCP and EK500 data, moving from the surface to depth (>300 m) at dawn and returning to the surface at dusk (SSL2) was clearly observed. This layer is a typical result of diel migration, as reported by numerous authors (Flagg and Smith, 1989; Nash *et al.*, 1989; Roe *et al.*, 1996; Herring *et al.*, 1998; etc). RMT samples showed that myctophid fish and decapod crustacea were undertaking vertical migration at the front (Howell, *pers comm.*). These animals represent dominant acoustic scattering groups, especially myctophid fish which have resonant gas bladders thereby augmenting their acoustic scattering (Johnson, 1977). Using a 500

μm mesh net, Thibault *et al.* (1994) reported the vertical migration of zooplankton over a depth range of 300-400 m, in agreement with the present observations.

A third layer of high acoustic backscatter (SSL3) was found coincident with the layer of subducted phytoplankton. LHPR samples identified an increase in abundance of euphausiids and chaetognaths at the depth of SSL3. These observations are supported by Baussant *et al.* (1993) who commented on similar scattering layers, and proposed that they were made up of euphausiid larvae present between 100 and 200 m depth in the frontal zone. SSL3 persisted despite and during the occurrence of diel migration. Owen (1981) and Wishner and Allison (1986) observed zooplankton concentrating in convergence zones as a result of the interruption of their diel migration. Frontal enhancement of zooplankton biomass may be caused by physical processes (such as the drawing down of surface species by subduction) and/or behaviour (active accumulation of animals at a more abundant food source, see section 1). The rate of subduction (25 m/day; Allen *et al.* 2001 -this issue) is significantly less than the rate of vertical migration of some zooplankton (Heywood, 1996). In addition the coincident abundance of phytoplankton tends to suggest the increase in zooplankton is a result of behaviourally mediated concentration in the presence of convergence zones and increased food abundance (as seen by Okubo, 1978; Gorsky *et al.*, 1991 and modelled by Franks, 1992; 1997).

In addition to the three identified scattering layers, a patch of high MVBS, seen in both 120 and 200 kHz EK500 backscatter, was constantly present at the surface on the Atlantic side of the Almeria-Oran front, coincident with the strong frontal jet (1 m/s). OPC data also indicated the presence of a high abundance of particles sized between 0.65 - 1.35 and 1.35 - 2.75 mm ESD. Thibault *et al.* (1994) and Seguin *et al.* (1994) both found an increase in the standing stock of zooplankton in the Almeria-Oran frontal jet. That increase was dominated by copepods with approximate lengths of 1 mm. These copepods would be ideally sampled by the OPC in the size range 0.65 – 1.35 mm ESD (Herman, 1992; following particle length approximately 1.5 times ESD according to Beaulieu *et al.*, 1999) and it is likely that the OPC data reflect their increased abundance in the frontal jet. The lack of diel migratory signal in both the acoustic and OPC data for this patch also agreed with previous observations. Seguin *et*

al. (1994) and Thibault *et al.* (1994) compared day and night net samples, taken with a 200 μm mesh, and found that there was no significant difference in abundance between them, implying that zooplankton in the 1-2 mm size range were not undertaking vertical migration in the Alboran Sea.

5. Conclusion.

Taken as a whole, these observations support the hypothesis presented by Gorsky *et al.* (1991), that enhanced superficial production can influence the mesopelagic ecosystem. It is likely that the observations in this study indicate that the horizontal and vertical distribution of larger zooplankton (e.g. > 5 mm in length) at the Almeria-Oran front are controlled by a combination of physical processes, with downward vertical motion providing a vertically displaced food source, and animal behaviour, with diel migration disturbed by food availability. The effects of mesoscale physical processes on zooplankton distribution/patchiness have similar temporal and spatial scales as some zooplankton behaviour (Haury, 1982), and as such can be difficult to differentiate in observations. Modern survey tools (SeaSoar, OPC, acoustics etc.) which determine physical and biological variables concurrently, and at the same high resolution time and space scales, permit an understanding of biological distributions about which previous investigators have had to speculate intuitively (Videau *et al.*, 1994; Baussant *et al.*, 1993). To identify ecosystem dynamics in the real ocean requires that relevant and complementary data are taken concurrently: the results of this study show convincingly that biological distributions in the vicinity of a front result from a combination of physical, chemical and biological factors.

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Figures:

Figure 1: a) The topography of the Alboran Sea (depths in metres): reproduced from the GEBCO digital atlas, BODC. b) NOAA-14 AVHRR image for the 13th October 1996 provided by the NERC through the Southampton Oceanography Centre and processed at the University of Pisa, Italy.

Figure 2. Cruise tracks for Fine Scale Surveys 1-3 (FSS1-3).

Figure 3: Contoured sections of temperature and salinity across the Almeria-Oran front. Leg e of FSS2 is shown here.

Figure 4: Contoured sections of fluorescence yield (instrument volts) across the Almeria-Oran front for Leg f of FSS2 (top) and FSS3 (middle), and light for FSS3 (bottom). Isopycnals 27.4 and 28.4 sigma-0 are overlaid for FSS3.

Figure 5: The vertical distribution of temperature (top), salinity (middle top), nitrate concentration (middle bottom) and fluorescence yield (bottom) from CTD stations across the Almeria-Oran front (from west to east).

Figure 6: Contoured sections of fluorescence yield (instrument volts - top), VM-ADCP acoustic backscatter amplitude (middle) and EK500 38 KHz acoustic backscatter amplitude (bottom), across the Almeria-Oran front for Leg g of FSS3. The 27.4 and 28.4 sigma-0 isopycnals are over-layed for reference.

Figure 7: The vertical distribution of zooplankton biovolume (from LHPR samples) and a contoured section of concurrent ADCP MVBS data.

Figure 8: Contoured sections of EK500 200 KHz MVBS (top), EK500 120 KHz MVBS (middle top), particle volume ratio size class 0.65-1.35 mm ESD (middle bottom), particle volume ratio size class 1.35-2.75 mm ESD (bottom) across the Almeria-Oran front for Leg f of FSS3. The 27.4 and 28.4 sigma-0 isopycnals are over-layed for reference.